Alpine Entomology 2 2018, 101–113 | DOI 10.3897/alpento.2.29250

PENSOFT

Alpine Entomology

Pollen host selection by predominantly alpine bee species of the genera *Andrena*, *Panurginus*, *Dufourea*, *Megachile*, *Hoplitis* and *Osmia* (Hymenoptera, Apoidea)

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http://zoobank.org/410B9230-C9CB-4E85-A038-0153A1369575

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Received 22 August 2018
Accepted 24 September 2018
Published 22 October 2018

Academic editor:
Jessica Litman

Key Words

Andrenidae
Apiformes
Halictidae
Megachilidae
mesolecty
oligolecty
pollen analysis
polylecty

Abstract

The pollen host selection by 19 bee species, which have their main Central European distribution in the Alps, was assessed by microscopical analysis of the scopal contents of about 900 females from museum and private collections. The results of the pollen analyses were complemented by a literature survey as well as by field observations. The examined species widely vary in pollen host spectrum and specialization, revealing a fascinating diversity in bee host plant use. Observed patterns of host plant choice range from narrow specialists, which exclusively collect pollen from the flowers of a single plant genus, to pronounced generalists, which harvest pollen from the flowers of up to 17 different plant families. A quantitative character is given to separate the morphologically very similar females of *Panurginus herzi* and *P. montanus*.

Zusammenfassung

Die Pollenwirtswahl von 19 Bienenarten, welche ihren zentraleuropäischen Verbreitungsschwerpunkt in den Alpen haben, wurde mittels mikroskopischer Analyse der Pollenladungen von rund 900 Weibchen aus Museums- und Privatsammlungen ermittelt. Die Ergebnisse der Pollenanalysen wurden durch eine Literaturauswertung sowie durch Feldbeobachtungen ergänzt. Die untersuchten Arten unterscheiden sich stark hinsichtlich Wirtspflanzenspektrum und Spezialisierungsgrad und umfassen sowohl enge Spezialisten, welche den Pollen ausschliesslich auf einer einzigen Pflanzengattung sammeln, als auch ausgeprägte Generalisten, welche bis zu 17 verschiedene Pflanzenfamilien als Pollenquellen nutzen. Ein quantitatives Merkmal zur Unterscheidung der äusserlich sehr ähnlichen Weibchen von *Panurginus herzi* und *P. montanus* wird gegeben.

Introduction

Bees are herbivores using nectar and pollen as the predominant food source for their larvae. While no floral specificity is known with respect to the collection of nectar, many bee species restrict pollen harvesting to closely related plant taxa (Robertson 1925, Westrich 1989). The degree of host plant specialization among bees widely varies: "monolectic" bee species are entirely dependent on the pollen of a single plant species even in the presence of sympatric species of the same genus, "oligolectic" species consistently collect pollen from flowers of a single plant genus, tribe or family, "mesolectic" species harvest pollen from flowers of two or three plant families and "polylectic" species exploit flowers of more than three plant families (Cane and Sipes 2006, Müller and

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Kuhlmann 2008). Even in polylectic species, host plant choice is usually limited to some degree and - as in more specialized taxa - governed by constraints with respect to pollen digestion, flower recognition or flower handling (Sedivy et al. 2008, Haider et al. 2014). Detailed knowledge of pollen host use is important for species conservation, the reconstruction of bee host range evolution and our understanding of the fascinating interrelationships between flowers and their pollinators.

The pollen host preferences of Western, Central and Northern European bee species are fairly well known thanks to several studies, which analyzed pollen loads of collected females by light microscopy (Chambers 1968, Raw 1974, Westrich 1989, Müller 1996, Michez et al. 2008, Müller and Kuhlmann 2008, Sedivy et al. 2008, 2013, Haider et al. 2014, Wood et al. 2016, Wood and Roberts 2017). Gaps of knowledge, however, exist for numerous species, which exclusively or predominantly occur in the Alps. Among the bee species, which have their main Central European distribution in the Alpine arc, pollen host preferences have been thoroughly analysed so far only for *Colletes floralis* Eversmann, *Colletes impunctatus* Nylander, *Anthidium montanum* Morawitz, *Chelostoma grande* (Nylander), *Hoplitis lepeletieri* (Pérez), *Hoplitis loti* (Morawitz) and *Hoplitis tuberculata* (Nylander) (Müller and Kuhlmann 2008, Müller 1996, 2015, Sedivy et al. 2008, 2013, Westrich 1989, 1993). For many other predominantly alpine species, information on host plant use either completely lacks, is based on field observations, which do not differentiate between nectar uptake and pollen collection, or relies on pollen analysis of female scopal loads without quantification, resulting in a list of pollen sources not considering their relative significance in the species' larval diet.

The present publication aims to fill the knowledge gap still existing on the host plant preferences of 19 predominantly alpine bee species, which are either endemic to the Alps or have a boreoalpine or boreomontane distribution. For that purpose, pollen stored in the scopae of females from museum and private collections originating from across the Alpine arc was removed and microscopically analysed.

Methods

The pollen host spectra of 19 bee species belonging to the six genera *Andrena* and *Panurginus* (Andrenidae), *Dufourea* (Halictidae) and *Megachile*, *Hoplitis* and *Osmia* (Megachilidae) were assessed by microscopical analysis of the scopal pollen contents of 877 female specimens deposited in museum and private collections and captured between the beginning of the 20th century and 2018. For each species, the aim was to analyze a minimum of 40 and a maximum of 50 pollen loads all originating from the Alpine arc. This goal was not attained for *Osmia alticola* Benoist and *Osmia steinmanni* Müller due to their rarity and poor representation in collections. For *Panurginus herzi* Morawitz, the pollen samples analysed by Vögeli (2001) were included in the present study and supplemented with numerous new samples. To account for potentially deviating pollen host use by specimens from different populations, pollen samples from females collected at as many different localities as possible were analysed. Specimens with identical information on the collection label (i.e. locality, date and collector) were regarded as originating from the same locality. Before removing pollen from the female scopae, the degree to which they were filled was estimated. The amount of pollen in the scopae was assigned to five classes, ranging from 1/5 (filled to one-fifth) to 5/5 (full load). The pollen grains were stripped off the scopae with a fine needle and embedded in glycerol gelatine on a microscopic slide. When a pollen load was composed of different pollen types, their percentages were estimated by counting the grains along two transects chosen randomly across the cover slip at a magnification of 400×. Pollen types represented by less than 5% of the counted grains were excluded to prevent a potential bias caused by contamination. For pollen loads consisting of two or more different pollen types, the proportion of the different types was corrected by their volume (Buchmann and O'Rourke 1991, Silveira 1991). For that purpose, the relative volumina of all pollen types within the sample were estimated by eye and the counted numbers of each type multiplied by a factor that corresponded to its volume. After assigning different weights to scopae according to their degree of filling (full loads were weighted five times more strongly than scopae filled to only one-fifth), the estimated percentages were summed up over all pollen samples for each species. To characterize the degree of host plant association, such as oligolecty, mesolecty or polylecty, definitions and methods proposed by Müller and Kuhlmann (2008) were applied. The pollen grains were identified down to family or, if possible, to subfamily, tribal or genus level at a magnification of 400× or 1000× with the aid of the literature cited in Westrich and Schmidt (1986), Beug (2004) and an extensive reference collection. Flower records written on the collection labels often facilitated pollen identification to a taxonomic level lower than the plant family. Difficult pollen types were identified by the palynologist Katharina Bieri (Biological Institute for Pollen Analysis, Kehrsatz). Certain closely related plant genera could not be properly identified with the method applied in the present study, such as *Sedum* and *Sempervivum* (Crassulaceae), *Fragaria* and *Potentilla* (Rosaceae), *Euphrasia* and *Rhinanthus* (Orobanchaceae) and *Campanula* and *Phyteuma* (Campanulaceae). Pollen grains of these taxa, however, were assigned to genus level if altitude, phenology or habitat excluded the alternative genus or if own field observations, literature data or label records all invariably suggest only one of the two genera. Such non-morphologically based pollen identifications are marked with "cf." in Table 1. The distinction of pollen from *Rhododendron* and *Vaccinium* (Ericaceae) and from *Euphrasia* and *Veronica* (Plantaginaceae) is difficult. For the former pair the thickness of the exine and for

the latter pair the shape of the swollen grains was used as distinctive characters. However, these characters could only be recognised in grains that were specifically oriented within the gelatine layer and/or completely swollen. If only typical *Rhododendron* (or *Vaccinium*) grains or typical *Euphrasia* (or *Veronica*) grains were present in a pollen sample, all grains for which the distinctive characters were not discernible were assigned to *Rhododendron* (or *Vaccinium*) and *Euphrasia* (or *Veronica*), respectively. Data based on a comprehensive literature survey on confirmed pollen hosts and observed flower visits as well as field observations made by the author during the last three decades were used to complement the results obtained by the microscopical analysis of scopal pollen loads.

The taxonomy of *Panurginus* in Central Europe is still under discussion. While the validity of *P. herzi* Morawitz as a biological species is undisputed, there is no consensus yet whether *P. sericatus* (Warncke) is a species of its own (e.g. Schwarz and Gusenleitner 1997, Amiet et al. 2010) or should rather be treated as a western subspecies of *P. montanus* Giraud (e.g. Warncke 1972, Ebmer 2001). No morphological characters are known to discriminate between the females of these latter two taxa. In contrast, the males slightly differ in the shape of the gonostylus (Amiet et al. 2010). However, there are populations in eastern Switzerland, which show an intermediate gonostylus shape (Amiet et al. 2010). Due to these morphological transitions, the two taxa are regarded as conspecific in the present study. The characters given by Amiet et al. (2010) to separate the females of *P. herzi* from those of *P. montanus* proved to be partly unreliable. The shape of the head, however, was recently found to be a reliable character allowing for the unambiguous identification of *P. herzi* (Hopfenmüller 2017). To quantify this character, the ratio of head length to head width (sensu Michener 2007) was measured under a stereomicroscope for 150 *Panurginus* females originating from 78 different localities in Switzerland, Austria and Germany. The measurements revealed an almost non-overlapping bimodal distribution in the head length to head width ratio (Fig. 1), corroborating the reliability of this character to separate the females of *P. herzi* and *P. montanus*. For the present study, *Panurginus* females with a head length to head width ratio of 0.76–0.82 were identified as *P. herzi* and those with a ratio of 0.84–0.90 as *P. montanus*. Pollen loads of females with a ratio of 0.83 were not considered for pollen analysis.

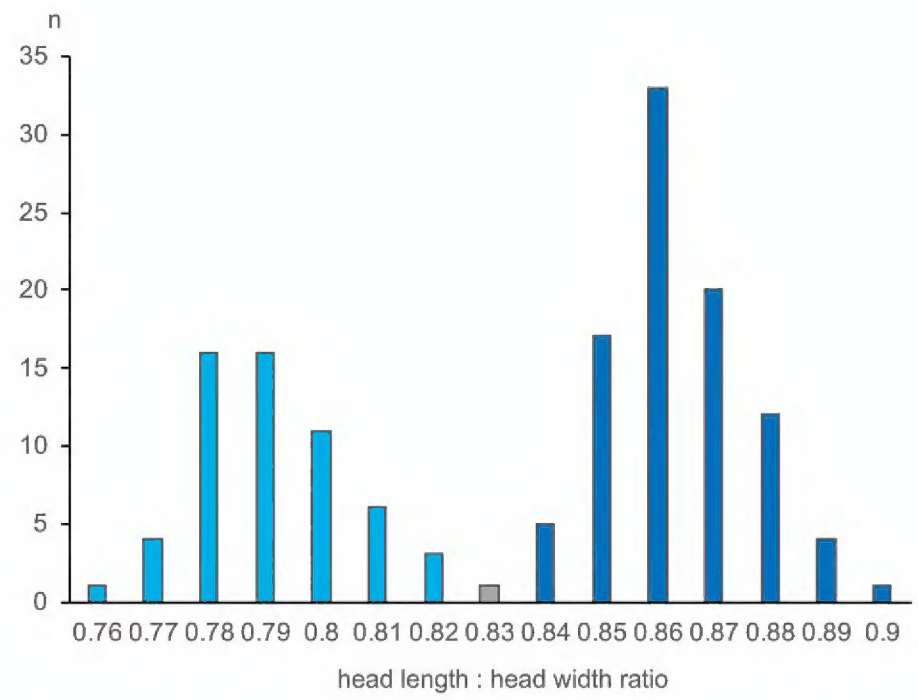


Figure 1. Head length to head width ratio in females of *Panurginus herzi* (light blue) and *P. montanus* (dark blue) (n = 150). Definitions for head length and head width according to Michener (2007).

Results

Andrena (*Andrena*) *fucata* Smith, 1847

Andrena fucata harvested the pollen of 17 plant families, among which Rosaceae, Apiaceae and *Helianthemum* (Cistaceae) predominated (Tab. 1, Fig. 2). Pollen of these three plant taxa contributed 77.7% to the total pollen grain volume. Herbs, shrubs and trees were among the exploited hosts (Tabs 1, 2), which suggests a high flexibility of the female bees to use different vegetation strata for pollen collection. The seven plant families listed by Chambers (1968) and Westrich (1989) as pollen hosts of *A. fucata* were all confirmed in the present study. Rhamnaceae were recently demonstrated to be an additional pollen source (Wood and Roberts 2017), and observations of flower visits on *Berberis* and *Lysimachia* (Stoeckhert 1933, Dylewska 1987, BWARS 2018) suggest that Berberidaceae and Primulaceae might be two further plant families occasionally exploited for pollen. The high significance of Rosaceae in the host plant spectrum of *A. fucata* as found in the present study is confirmed by two British studies, which identified Rosaceae pollen to be the most important constituent of the collected pollen, representing 80.3% and 57.9%, respectively, of the total pollen grain volume (Chambers 1968, Wood and Roberts 2017). According to several authors, *Rubus idaeus* L. is a preferred pollen host among the Rosaceae (Alfken 1913, Stoeckhert 1933, Amiet et al. 2010).

Andrena (*Andrena*) *lapponica* Morawitz, 1872

Andrena lapponica had the narrowest pollen diet among the three *Andrena* species of the subgenus *Andrena* investigated in the present study. Although it collected the pollen of 16 plant families (Tab. 1), flowers of the Ericaceae were strongly preferred. Among the Ericaceae, both *Vaccinium* and *Rhododendron* were exploited. As revealed by field observations, *Vaccinium myrtillus* L. is the most important pollen host in the Swiss Alps (Fig. 3), albeit the pollen of other *Vaccinium* species such as *V. vitis-idaea* L., *V. uliginosum* L. or *V. oxycoccos* L. is occasionally also collected (Stoeckhert 1933, Westrich 1989). As the flowering period of the main host is short and hardly extends over a period of more than few weeks, many of the alternative non-Ericaceae hosts might have acted as replacement pollen sources before and after the

Table 1. Pollen host spectrum of 19 predominantly alpine bee species of the genera *Andrena* and *Panurginus* (Andrenidae), *Dufourea* (Halictidae) and *Megachile*, *Hoplitis* and *Osmia* (Megachilidae). Subgeneric classification according to Michener (2007). n = total number of pollen loads, N = number of pollen loads from different localities. Countries: A = Austria, CH = Switzerland, D = Germany, F = France, FL = Liechtenstein, IT = Italy. Plant families: ACE = Aceraceae, ALL = Alliaceae, API = Apiaceae, AQU = Aquifoliaceae, ASP = Asparagaceae, AST = Asteraceae, BER = Berberidaceae, BOR = Boraginaceae, BRA = Brassicaceae, CAM = Campanulaceae, CAP = Caprifoliaceae, CAR = Caryophyllaceae, CIS = Cistaceae, CLU = Clusiaceae, COR = Cornaceae, CRA = Crassulaceae, DIP = Dipsacaceae, ERI = Ericaceae, EUP = Euphorbiaceae, FAB = Fabaceae, GEN = Gentianaceae, GER = Geraniaceae, JUN = Juncaceae, LAM = Lamiaceae, LIL = Liliaceae, LIN = Linaceae, ORO = Orobanchaceae, OXA = Oxalidaceae, PLA = Plantaginaceae, POL = Polygonaceae, PRI = Primulaceae, PYR = Pyrolaceae, RAN = Ranunculaceae, RES = Resedaceae, RHA = Rhamnaceae, ROS = Rosaceae, SAL = Salicaceae, SAN = Santalaceae, SAX = Saxifragaceae, SCR = Scrophulariaceae, TIL = Tiliaceae. Definitions of bee host ranges after Müller and Kuhlmann (2008).

Bee species	n	N	Origin (and number) of pollen loads	% pollen grain volume (number of loads)	Preferred host(s)	% pollen grain volume of preferred host	% pure loads of preferred host	% loads with preferred host	Host range
Andrena (*Andrena*) *fucata* Smith, 1847	50	40	CH (48), D (1), IT (1)	ROS (other) 41.3% (34), ROS (*Sanguisorba officinalis*) 1.7% (2), ROS (cf. *Potentilla*) 0.4% (2), API 17.6% (16), CIS (*Helianthemum*) 16.6% (14), CAP (*Lonicera*) 4.3% (2), PLA (*Plantago*) 4.2% (7), BRA 2.8% (1), CAM 2.1% (1), POL (*Polygonum bistorta*) 2.0% (2), RAN 1.6% (1), ACE (*Acer*) 1.4% (1), AQU (*Ilex*) 1.0% (1), JUN 1.0% (2), COR (*Cornus*) 0.5% (1), AST (Carduoideae) 0.4% (1), ERI (*Vaccinium*) 0.4% (1), EUP (*Euphorbia*) 0.2% (1), SAN (*Thesium*) 0.2% (1), unknown 0.3% (2)	Rosaceae, Apiaceae and *Helianthemum*	77.7%	58.0%	92.0%	polylectic (17 plant families) with affinity for Rosaceae, Apiaceae and *Helianthemum* (Cistaceae)
Andrena (*Andrena*) *lapponica* Morawitz, 1872	50	46	CH (49), FL (1)	ERI (*Vaccinium*) 75.7% (41), ERI (*Rhododendron*) 5.8% (5), ROS (cf. *Potentilla*) 0.9% (6), ROS (*Geum*) 0.6% (1), ROS (other) 2.1% (3), AST (Carduoideae) 2.4% (1), AST (Asteroideae) 0.4% (1), PYR (*Moneses*) 1.9% (1), CIS (*Helianthemum*) 1.5% (1), RAN 1.4% (1), PRI (*Soldanella*) 1.3% (2), OXA (*Oxalis*) 1.2% (3), SAL (*Salix*) 1.1% (4), CAR 0.8% (1), LIL 0.6% (1), PLA (*Plantago*) 0.4% (2), SAX (*Saxifraga*) 0.2% (1), ACE (*Acer*) 0.1% (1), LAM (Nepetoidea) 0.1% (1), GEN 0.1% (1), unknown 1.4% (4)	Ericaceae	81.5%	58.0%	92.0%	polylectic (16 plant families) with strong preference for Ericaceae
Andrena (*Andrena*) *rogenhoferi* Morawitz, 1872	50	47	CH (42), A (3), D (2), F (2), FL (1)	GEN (cf. *Gentiana*) 18.0% (12), SAX (*Saxifraga*) 17.2% (13), CIS (*Helianthemum*) 13.7% (12), ERI (*Rhododendron*) 9.3% (8), ERI (*Vaccinium*) 3.5% (2), SAL (*Salix*) 9.5% (7), ROS (*Geum*) 2.6% (3), ROS (cf. *Potentilla*) 0.1% (1), ROS (other) 4.8% (9), ACE (*Acer*) 7.1% (5), TIL (*Tilia*) 3.9% (4), API 3.4% (6), CAM 1.2% (4), RAN (*Pulsatilla*) 1.1% (1), BER (*Berberis*) 1.0% (2), CRA 0.5% (1), AST (Cichorioideae) 0.3% (2), BRA 0.2% (1), CAP (*Lonicera*) 0.2% (1), RHA (*Frangula*) 0.1% (1), unknown 2.3% (4)	–	–	–	–	polylectic (17 plant families)
Andrena (*Cnemidandrena*) *freygessneri* Alfken, 1904	50	29	CH (43), IT (5), A (1), F (1)	CRA (cf. *Sempervivum*) 78.2% (42), SAX (*Saxifraga*) 5.7% (8), CIS (*Helianthemum*) 5.5% (6), LAM (Nepetoideae) 2.4% (4), ROS (cf. *Potentilla*) 1.5% (4), ROS (other) 0.9% (2), AST (Asteroideae) 1.7% (4), ERI (*Calluna*) 1.2% (1), GEN 1.1% (2), BRA 0.9% (1), CAR 0.6% (3), unknown 0.3% (1)	*Sempervivum*	78.2%	54.0%	84.0%	polylectic (10 plant families) with strong preference for *Sempervivum* (Crassulaceae)
Andrena (*Oreomelissa*) *coitana* (Kirby, 1802)	50	41	CH (44), A (4), D (1), FL (1)	AST (Carduoideae) 10.2% (11), AST (Cichorioideae) 8.6% (14), AST (Asteroideae) 5.8% (8), CAM 24.2% (18), ROS (cf. *Potentilla*) 14.2% (19), ROS (*Sanguisorba officinalis*) 0.9% (1), ROS (other) 3.2% (5), CIS (*Helianthemum*) 6.0% (6), API 6.0% (8), SCR 5.7% (8), LAM (Lamioideae) 3.7% (4), LAM (Nepetoideae) 1.6% (3), ORO (cf. *Euphrasia*) 3.5% (5), CRA 2.6% (2), PLA (*Veronica*) 1.8% (3), PLA (*Plantago*) 0.6% (1), GEN 0.8% (1), RAN 0.3% (2), unknown 0.3% (5)	–	–	–	–	polylectic (12 plant families)
Panurginus herzi Morawitz, 1891	50	27	CH (48), A (1), D (1)	ROS (cf. *Potentilla*) 99.2% (50), CIS (*Helianthemum*) 0.5% (1), ERI (*Vaccinium*) 0.3% (1)	*Potentilla*	99.2%	96.0%	100%	narrowly oligolectic on *Potentilla* (Rosaceae)
Panurginus montanus Giraud, 1861	50	35	CH (47), FL (3)	ROS (cf. *Potentilla*) 50.4% (39), CIS (*Helianthemum*) 39.3% (31), RAN 2.8% (9), BRA 2.3% (3), ORO (cf. *Euphrasia*) 1.6% (2), CAR 1.5% (4), SAX (*Saxifraga*) 0.3% (1), CRA 0.3% (1), API 0.3% (1), AST (Cichorioideae) 0.2% (2), unknown 1.0% (1)	*Potentilla* and *Helianthemum*	89.7%	66.0%	98.0%	polylectic (10 plant families) with affinity for *Potentilla* (Rosaceae) and *Helianthemum* (Cistaceae)

Bee species	n	N	Origin (and number) of pollen loads	% pollen grain volume (number of loads)	Preferred host(s)	% pollen grain volume of preferred host	% pure loads of preferred host	% loads with preferred host	Host range
Dufourea alpina Morawitz, 1865	50	35	CH (41), FL (9)	CAM 80.1% (46), AST (Cichorioideae) 7.8% (22), ORO (cf. *Euphrasia*) 6.1% (10), CIS (*Helianthemum*) 2.7% (2), LAM (Nepetoideae) 1.7% (3), CAR 1.1% (4), LIN (*Linum*) 0.5% (1)	Campanulaceae	80.1%	42.0%	92.0%	polylectic (7 plant families) with strong preference for Campanulaceae
Dufourea paradoxa (Morawitz, 1867)	46	36	CH (42), A (1), F (1), IT (2)	CRA 26.4% (16), ORO (cf. *Euphrasia*) 24.7% (21), LAM (Nepetoideae) 12.6% (13), CIS (*Helianthemum*) 9.6% (9), AST (Cichorioideae) 4.9% (9), AST (Carduoideae) 2.4% (3), AST (Asteroideae) 2.0% (4), CAR 9.2% (14), GEN 4.2% (4), ROS (cf. *Potentilla*) 2.1% (5), PRI (*Soldanella*) 1.0% (1), SAX (*Saxifraga*) 0.5% (1), SAL (*Salix*) 0.1% (1), FAB 0.1% (1), CAM 0.1% (1), unknown 0.1% (1)	–	–	–	–	polylectic (13 plant families)
Megachile (*Megachile*) *alpicola* Alfken, 1924	50	50	CH (40), A (1), D (9)	FAB (*Lotus*) 33.3% (33), FAB (*Trifolium*) 3.2% (3), FAB (Genisteae) 2.7% (1), FAB (*Medicago*) 0.5% (2), FAB (*Vicia/Lathyrus*) 0.4% (1), FAB (other) 3.9% (3), AST (Cichorioideae) 13.2% (16), AST (Asteroideae) 12.8% (13), AST (Carduoideae) 4.4% (4), CIS (*Helianthemum*) 4.6% (7), ASP (*Anthericum*) 4.2% (1), BRA 2.7% (2), RAN 2.5% (4), CLU (*Hypericum*) 2.0% (3), CRA 2.0% (4), ORO (*Odontites*) 1.7% (1), PLA (*Veronica*) 1.5% (1), ALL (*Allium*) 1.3% (2), ROS (cf. *Potentilla*) 0.9% (2), DIP (*Scabiosa*) 0.8% (1), LAM (Nepetoideae) 0.4% (1), SAL (*Salix*) 0.2% (1), CAM 0.1% (1), unknown 0.7% (4)	Fabaceae and Asteraceae	74.5%	44.0%	44%	polylectic (16 plant families) with affinity for Fabaceae and Asteraceae
Megachile (*Xanthosarus*) *analis* Nylander, 1852	50	49	CH (48), D (1), IT (1)	CAM 61.6% (36), FAB (*Lotus*) 25.0% (26), FAB (*Hippocrepis*) 5.1% (7), FAB (*Onobrychis*) 3.6% (2), CIS (*Helianthemum*) 3.1% (2), ORO (*Odontites*) 1.1% (1), RES (*Reseda*) 0.4% (1), CRA 0.1% (1)	Campanulaceae and Fabaceae	95.3%	92.0%	100%	mesolectic on Campanulaceae and Fabaceae
Hoplitis (*Anthocopa*) *villosa* (Schenck, 1853)	50	46	CH (44), F (4), A (1), D (1)	AST (Cichorioideae) 72.8% (46), AST (Carduoideae) 22.4% (16), AST (Asteroideae) 0.3% (3), GER (*Geranium*) 2.4% (2), CIS (*Helianthemum*) 2.1% (5)	Cichorioideae and Carduoideae	95.2%	88.0%	100%	broadly oligolectic on Cichorioideae and Carduoideae (Asteraceae)
Osmia (*Helicosmia*) *labialis* Pérez, 1879	50	48	CH (46), D (2), F (2)	AST (Carduoideae) 95.7% (48), AST (Cichorioideae) 2.6% (4), AST (Asteroideae) 1.5% (1), CIS (*Helianthemum*) 0.2% (1)	Carduoideae	95.7%	90.0%	96%	broadly oligolectic on Carduoideae (Asteraceae)
Osmia (*Melanosmia*) *alticola* Benoist, 1922	16	15	CH (16)	FAB (*Lotus*) 38.4% (12), FAB (*Hippocrepis*) 36.0% (7), FAB (*Anthyllis*) 8.8% (3), FAB (*Trifolium*) 5.5% (2), FAB (other) 11.1% (2), unknown 0.2% (1)	Fabaceae	99.8%	93.8%	100%	broadly oligolectic on Fabaceae
Osmia (*Melanosmia*) *inermis* (Zetterstedt, 1838)	50	43	CH (41), A (7), D (2)	FAB (*Lotus*) 70.4% (45), FAB (*Hippocrepis*) 20.0% (17), FAB (*Anthyllis*) 1.3% (3), ERI (*Vaccinium*) 5.0% (2), ROS (cf. *Potentilla*) 1.7% (1), LAM (Lamioideae) 1.6% (1)	Loteae (*Anthyllis*, *Hippocrepis*, *Lotus*)	91.7%	92.0%	96.0%	polylectic (4 plant families) with strong preference for Loteae (Fabaceae)
Osmia (*Melanosmia*) *parietina* Curtis, 1828	50	44	CH (50)	FAB (*Lotus*) 61.6% (48), FAB (*Hippocrepis*) 22.5% (25), FAB (*Trifolium*) 7.4% (11), FAB (*Anthyllis*) 1.4% (2), LAM (Lamioideae) 2.4% (2), LAM (Nepetoideae) 1.5% (2), CIS (*Helianthemum*) 1.9% (2), ROS (cf. *Potentilla*) 1.0% (2), GEN 0.3 (1)	Loteae (*Anthyllis*, *Hippocrepis*, *Lotus*)	85.5%	72.0%	100%	polylectic (5 plant families) with strong preference for Loteae (Fabaceae)
Osmia (*Melanosmia*) *steinmanni* Müller, 2002	15	6	CH (14), F (1)	FAB (*Lotus*) 61.9% (13), FAB (*Hippocrepis*) 34.4% (9), FAB (*Trifolium*) 1.5% (1), ERI (*Rhododendron*) 2.2% (1)	Loteae (*Hippocrepis*, *Lotus*)	96.3%	86.7%	100%	probably mesolectic on Fabaceae and Ericaceae with strong preference for Loteae (Fabaceae)
Osmia (*Melanosmia*) *uncinata* Gerstaecker, 1869	50	41	CH (43), D (4), A (1), FL (1), IT (1)	FAB (*Lotus*) 46.4% (38), FAB (*Hippocrepis*) 11.4% (19), FAB (*Trifolium*) 7.9% (12), FAB (*Onobrychis*) 3.4% (3), FAB (*Medicago*) 2.8% (4), FAB (*Vicia/Lathyrus*) 1.9% (2), FAB (*Anthyllis*) 1.7% (1), FAB (other) 2.2% (6), ROS (cf. *Potentilla*) 3.6% (3), ROS (other) 6.3% (3), LAM (Lamioideae) 6.3% (5), LAM (Nepetoideae) 0.6% (1), PLA (*Plantago*) 1.3% (5), PLA (*Veronica*) 0.3% (1), ALL (*Allium*) 1.2% (2), RAN 0.8% (2), CAP (*Lonicera*) 0.7% (1), GEN 0.3% (1), BOR (*Echium*) 0.3% (1), CRA 0.1% (1), CIS (*Helianthemum*) 0.1% (1), unknown 0.4% (1)	Fabaceae	77.7%	56.0%	90.0%	polylectic (11 plant families) with strong preference for Fabaceae
Osmia (*Melanosmia*) *xanthomelana* (Kirby, 1802)	50	50	CH (44), F (3), IT (3)	FAB (*Hippocrepis*) 83.4% (49), FAB (*Lotus*) 16.6% (21)	*Hippocrepis* and *Lotus*	100%	100%	100%	narrowly oligolectic on *Hippocrepis* and *Lotus* (Fabaceae)

bloom of *V. myrtillus*. However, several records of *A. lapponica* from Switzerland originate from localities lacking larger Ericaceae stands, which suggests that this species might occasionally also reproduce in the absence of *Vaccinium* or *Rhododendron*. In fact, a strong population of *A. lapponica* exists on Mt. Snežnik in southern Slovenia, where Ericaceae are completely lacking (Gogala 2011). Here, pollen is collected on *Helianthemum* (Cistaceae) and *Salix* (Salicaceae). Thus, the pollen specialization of *A. lapponica* appears to be less strict than was formerly assumed, e.g. by Westrich (1989).

Andrena (*Andrena*) *rogenhoferi* Morawitz, 1872

Andrena rogenhoferi harvested the pollen of 17 plant families (Tab. 1). As in *A. fucata*, pollen was collected on herbs, shrubs and trees (Tabs 1, 2). Important host plant taxa, whose pollen contributed 10% or more to the total pollen grain volume, were *Gentiana* (Gentianaceae), *Saxifraga* (Saxifragaceae, Fig. 4), *Helianthemum* (Cistaceae), Ericaceae and *Salix* (Salicaceae). As revealed by literature data, label records and field observations, species among these main host plant taxa known to be exploited for pollen are *Gentiana acaulis* L., *G. lutea* L. and *G. punctata* L. (Alfken 1942, Stoeckhert 1954, Dylewska 1987), *Saxifraga aizoides* L., *S. oppositifolia* L., *S. rudolphiana* Hornsch. and *S. sedoides* L. (Frey-Gessner 1899–1907, Alfken 1942, Stoeckhert 1954, Dylewska 1987, 1993, Kreisch 1996, Ebmer 2003, Zettel et al. 2008), *Helianthemum nummularium* (L.) Mill., *Rhododendron ferrugineum* L. (Dylewska 1993), *Vaccinium vitis-idaea* L. (Ebmer 1997) and *Salix helvetica* Vill., *S. reticulata* L. and *S. waldsteiniana* Willd. (Schedl 1982, Ebmer 1997).

Andrena (*Cnemidandrena*) *freygessneri* Alfken, 1904

Andrena freygessneri collected the pollen of 10 plant families (Tab. 1). However, it exhibited a strong preference for Crassulaceae. Field observations indicate that species of *Sempervivum*, such as *S. arachnoideum* L., *S. montanum* L. and *S. tectorum* L., are the main or even the exclusive hosts among the Crassulaceae (Fig. 5). As Crassulaceae pollen cannot reliably be assigned to genus level by the method applied in the present study, it cannot be excluded that other Crassulaceae taxa, such as *Sedum*, are occasionally also exploited. The preference for *Sempervivum* as demonstrated by this study is supported by observations by De Beaumont (1958), Ebmer et al. (1994), Ebmer (2001, 2003) and Amiet et al. (2010), who recorded *A. freygessneri* visiting flowers of *Sempervivum* in the Swiss and Austrian Alps.

Andrena (*Oreomelissa*) *coitana* (Kirby, 1802)

Andrena coitana harvested the pollen of 12 plant families (Tab. 1). More than 95% of the pollen recorded in the female scopae originated from herbs (Tabs 1, 2), suggesting that the species usually does not collect pollen on shrubs and trees except for *Rubus* (Rosaceae), but restricts pollen harvesting to the herbal layer. Important host plant taxa, whose pollen represented more than 10% of the total pollen grain volume, were Asteraceae (Fig. 6), Campanulaceae and Rosaceae. All three subfamilies of the Asteraceae were exploited and *Potentilla* was the most important host among the Rosaceae. Literature data, label records and field observations indicate that among the Campanulaceae flowers of *Campanula*, *Jasione* and *Phyteuma* are all exploited for pollen (Tab. 2). Chambers (1968) and Westrich (1989) list pollen hosts belonging to five and seven plant families, respectively, among which only Caryophyllaceae were not recorded in the pollen loads analysed in the present study.

Panurginus herzi Morawitz, 1891

Panurginus herzi exclusively collected pollen on *Potentilla* (Rosaceae) except for two specimens, whose pollen loads additionally contained marginal amounts of pollen of *Helianthemum* (Cistaceae) and *Vaccinium* (Ericaceae), respectively (Tab. 1). Field observations revealed that *Potentilla aurea* L. and *P. erecta* (L.) Raeusch. are among the most important pollen hosts in the Swiss Alps (Fig. 7). These results are in line with Vögeli (2001), who supposed *P. herzi* to be a *Potentilla* oligolege, and with Romankova and Astafurova (2011), who mention a flower visiting record of *P. herzi* on *Potentilla chrysantha* Trevir. in western Siberia.

Panurginus montanus Giraud, 1861

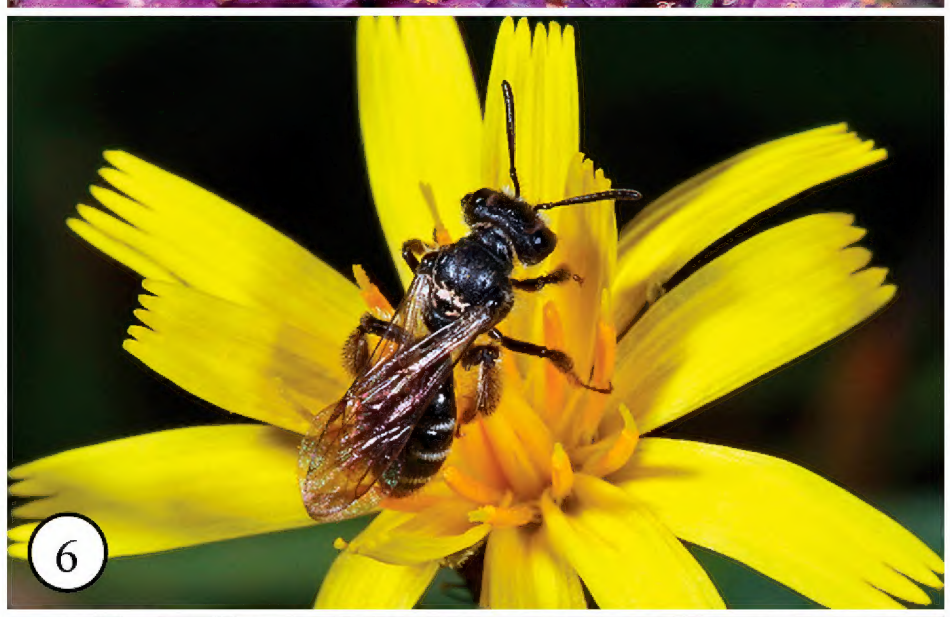
Panurginus montanus had a distinctly broader diet than *P. herzi* and collected the pollen of 10 plant families (Tab. 1, Fig. 8). *Potentilla* (Rosaceae) and *Helianthemum* (Cistaceae) were by far the most important hosts. Pollen of these two taxa contributed 89.7% to the total pollen grain volume. As numerous pollen loads contained mixtures of *Potentilla* and *Helianthemum* pollen, the existence of two cryptic species each specialized to a different host can be excluded. The results of this study contradict the assumption that *P. montanus* is specialized to Asteraceae (Westrich 1989). Blüthgen (1952) observed several females visiting the flowers of *Geranium sylvaticum* L. (Geraniaceae), suggesting that *Geranium* might be an additional pollen host.

Dufourea alpina Morawitz, 1865

Dufourea alpina collected the pollen of 7 plant families (Tab. 1), but exhibited a strong preference for the pollen of Campanulaceae (Fig. 9). Field observations showed that among the Campanulaceae flowers of both *Campanula* and *Phyteuma* are exploited for pollen. These results support Friese (1898) and Westrich (1989), who assumed a preference of pollen collecting females of *D. alpina* for *Phyteuma* and *Campanula*, respectively.

Dufourea paradoxa (Morawitz, 1867)

Dufourea paradoxa had a distinctly broader diet than *D. alpina* and collected the pollen of 13 plant families, among which Crassulaceae, Orobanchaceae and Lamiaceae predominated (Tab. 1). Pollen of these three plant families contributed 63.7% to the total pollen grain volume. Literature data, label records and field observations indicate



Figures 2–9. (**2**) *Andrena fucata* on Apiaceae spec. (photo S. Falk). (**3**) *Andrena lapponica* on *Vaccinium myrtillus* L. (photo P. Westrich). (**4**) *Andrena rogenhoferi* on *Saxifraga rudolphiana* Hornsch. (photo W. Kreisch). (**5**) *Andrena freygessneri* on *Sempervivum arachnoideum* L. (photo D. Bénon, www.swisswildbees.ch). (**6**) *Andrena coitana* on *Leontodon autumnalis* L. (photo H.-J. Martin). (**7**) *Panurginus herzi* on *Potentilla aurea* L. (**8**) *Panurginus montanus* on *Gypsophila repens* L. (**9**) *Dufourea alpina* on *Phyteuma betonicifolium* Vill.

Table 2. Confirmed or most probable pollen host genera of 19 predominantly alpine bee species of the genera *Andrena* and *Panurginus* (Andrenidae), *Dufourea* (Halictidae) and *Megachile*, *Hoplitis* and *Osmia* (Megachilidae) based on the present study (= p.s.) and the literature. Subgeneric classification according to Michener (2007). The plant families are arranged according to their significance in the species' pollen host spectrum (see Tab. 1), the plant genera within each family are arranged in alphabetical order.

Bee species	Pollen host genera
Andrena (*Andrena*) *fucata* Smith, 1847	**Rosaceae:** *Crataegus* (Stoeckhert 1933, BWARS 2018), *Fragaria* (Dylewska 1987), *Potentilla* (Chambers 1968, Westrich 1989, p.s.), *Prunus* (BWARS 2018), *Rosa* (Chambers 1968, Westrich 1989, Dylewska 1993), *Rubus* (Alfken 1913, Stoeckhert 1933, Chambers 1968, Westrich 1989, Dylewska 1993, Ebmer 2003, Amiet et al. 2010), *Sanguisorba* (p.s.); **Apiaceae:** *Chaerophyllum* (Chambers 1968, Westrich 1989); *Oenanthe* (BWARS 2018); **Cistaceae:** *Helianthemum* (Chambers 1968, Westrich 1989, p.s.); **Caprifoliaceae:** *Lonicera* (p.s.); **Plantaginaceae:** *Plantago* (p.s.), *Veronica* (Chambers 1968, Westrich 1989); **Brassicaceae:** *Barbarea* (Chambers 1968, Westrich 1989), *Brassica* (Westrich 1989), *Sinapis* (Chambers 1968, Westrich 1989); **Campanulaceae:** *Jasione* (Stoeckhert 1933); **Polygonaceae:** *Polygonum* (p.s.), *Rumex* (Chambers 1968); **Ranunculaceae:** *Ranunculus* (Chambers 1968, Westrich 1989); **Aceraceae:** *Acer* (Wood and Roberts 2017, p.s.); **Aquifoliaceae:** *Ilex* (Wood and Roberts 2017, p.s.); **Cornaceae:** *Cornus* (p.s.); **Asteraceae:** *Crepis* (Dylewska 1987), *Taraxacum* (Dylewska 1987), *Tussilago* (Frey-Gessner 1899–1907); **Ericaceae:** *Vaccinium* (BWARS 2018, p.s.); **Euphorbiaceae:** *Euphorbia* (BWARS 2018, p.s.); **Santalaceae:** *Thesium* (p.s.); **Rhamnaceae:** *Frangula* (Stoeckhert 1933); **Berberidaceae:** *Berberis* (Stoeckhert 1933, Dylewska 1987); **Primulaceae:** *Lysimachia* (BWARS 2018).
Andrena (*Andrena*) *lapponica* Morawitz, 1872	**Ericaceae:** *Rhododendron* (Frey-Gessner 1899–1907, Pittioni and Schmidt 1943, Dylewska 1993, p.s.), *Vaccinium* (Frey-Gessner 1899–1907, Stoeckhert 1933, Westrich 1989, Dylewska 1993, p.s.); **Rosaceae:** *Filipendula* (Pittioni and Schmidt 1943), *Geum* (p.s.), *Potentilla* (p.s.), *Rosa* (Dylewska 1993), *Rubus* (Ebmer 2003); **Asteraceae:** *Hieracium* (Dylewska 1993), *Taraxacum* (Dylewska 1993, Westrich 1989); **Pyrolaceae:** *Moneses* (p.s.); **Cistaceae:** *Helianthemum* (Ebmer 2003, Gogala 2011, p.s.); **Primulaceae:** *Soldanella* (p.s.); **Oxalidaceae:** *Oxalis* (p.s.); **Salicaceae:** *Salix* (Dylewska 1993, Gogala 2011, p.s.); **Plantaginaceae:** *Plantago* (p.s.); *Veronica* (Westrich 1989); **Saxifragaceae:** *Saxifraga* (Frey-Gessner 1899–1907, p.s.); **Aceraceae:** *Acer* (p.s.).
Andrena (*Andrena*) *rogenhoferi* Morawitz, 1872	**Gentianaceae:** *Gentiana* (Alfken 1942, Stoeckhert 1954, Dylewska 1987, p.s.); **Saxifragaceae:** *Saxifraga* (Frey-Gessner 1899–1907, Alfken 1942, Stoeckhert 1954, Dylewska 1987, 1993, Kreisch 1996, Ebmer 2003, Zettel et al. 2008, p.s.); **Cistaceae:** *Helianthemum* (Ebmer 2003, p.s.); **Ericaceae:** *Rhododendron* (Frey-Gessner 1899–1907, Dylewska 1987, 1993, Westrich 1989, p.s.), *Vaccinium* (Ebmer 1997, p.s.); **Salicaceae:** *Salix* (Schedl 1982, Dylewska 1993, Ebmer 1997, Gogala 2011 p.s.); **Rosaceae:** *Dryas* (Ebmer 2003, Zettel et al. 2008), *Geum* (p.s.), *Potentilla* (Franz 1982, p.s.), *Rosa* (Gogala 2011); **Aceraceae:** *Acer* (Westrich 1989, p.s.); **Tiliaceae:** *Tilia* (p.s.); **Apiaceae:** *Astrantia* (Zettel et al. 2008); **Ranunculaceae:** *Pulsatilla* (p.s.); **Berberidaceae:** *Berberis* (Frey-Gessner 1899–1907, Dylewska 1987, 1993, p.s.); **Asteraceae:** *Taraxacum* (Trautmann and Trautmann 1924, Ebmer 1997); **Caprifoliaceae:** *Lonicera* (p.s.); **Rhamnaceae:** *Frangula* (p.s.).
Andrena (*Cnemidandrena*) *freygessneri* Alfken, 1904	**Crassulaceae:** *Sempervivum* (De Beaumont 1958, Ebmer et al. 1994, Ebmer 2001, 2003, Amiet et al. 2010, p.s.); **Saxifragaceae:** *Saxifraga* (Frey-Gessner 1899–1907, p.s); **Cistaceae:** *Helianthemum* (Ebmer 2001, p.s.); **Lamiaceae:** *Thymus* (p.s.); **Rosaceae:** *Potentilla* (p.s.); **Ericaceae:** *Calluna* (p.s.).
Andrena (*Oreomelissa*) *coitana* (Kirby, 1802)	**Asteraceae:** *Achillea* (Peeters et al. 2012), *Centaurea* (Stoeckhert 1933, Chambers 1968, Dylewska 1993, Westrich 1989, Falk and Lewington 2015), *Cichorium* (Stoeckhert 1933, Westrich 1989), *Cirsium* (Chambers 1968, Westrich 1989, Falk and Lewington 2015), *Crepis* (Chambers 1968, Westrich 1989, Falk and Lewington 2015), *Hieracium* (Stoeckhert 1933, Dylewska 1993), *Hypochoeris* (Falk and Lewington 2015), *Leontodon* (Chambers 1968, Westrich 1989, Dylewska 1993), *Picris* (Westrich 1989), *Senecio* (Falk and Lewington 2015), *Solidago* (Stoeckhert 1933); **Campanulaceae:** *Campanula* (Stoeckhert 1933, Chambers 1968, Westrich 1989, Falk and Lewington 2015), *Jasione* (Westrich 1989), *Phyteuma* (p.s.); **Rosaceae:** *Potentilla* (Stoeckhert 1933, Westrich 1989, Falk and Lewington 2015, p.s), *Rosa* (Dylewska 1993), *Rubus* (Stoeckhert 1933, Chambers 1968, Peeters et al. 2012), *Sanguisorba* (p.s.); **Cistaceae:** *Helianthemum* (p.s.); **Apiaceae:** *Angelica* (Westrich 1989, Peeters et al. 2012), *Daucus* (Stoeckhert 1933, Westrich 1989), *Heracleum* (Stoeckhert 1933, Chambers 1968, Westrich 1989, Falk and Lewington 2015); **Lamiaceae:** *Prunella* (Stoeckhert 1933), *Salvia* (Westrich 1989); **Orobanchaceae:** *Euphrasia* (Stoeckhert 1933, Westrich 1989, p.s.); **Plantaginaceae:** *Plantago* (p.s.), *Veronica* (p.s.); **Gentianaceae:** *Centaurium* (Chambers 1968); **Ranunculaceae:** *Ranunculus* (Falk and Lewington 2015); **Caryophyllaceae:** *Dianthus* (Westrich 1989), *Stellaria* (Falk and Lewington 2015).
Panurginus herzi Morawitz, 1891	**Rosaceae:** *Potentilla* (p.s.); **Cistaceae:** *Helianthemum* (p.s.); **Ericaceae:** *Vaccinium* (p.s.)
Panurginus montanus Giraud, 1861	**Rosaceae:** *Potentilla* (Dylewska 1993, p.s.); **Cistaceae:** *Helianthemum* (p.s.); **Ranunculaceae:** *Ranunculus* (Dylewska 1993); **Orobanchaceae:** *Euphrasia* (p.s.); **Caryophyllaceae:** *Gypsophila* (p.s.); **Saxifragaceae:** *Saxifraga* (p.s.); **Asteraceae:** *Hieracium* (Dylewska 1993), *Leontodon* (Dylewska 1993).
Dufourea alpina Morawitz, 1865	**Campanulaceae:** *Campanula* (Ebmer 1984, Westrich 1989, Dylewska 1993, p.s.), *Phyteuma* (Friese 1898, Ebmer 2003, Bossert 2014, p.s.); **Asteraceae:** *Hieracium* (Ebmer 1984, Westrich 1989), *Leontodon* (Schedl 1982, Bossert 2014), *Solidago* (Stoeckhert 1954); **Orobanchaceae:** *Euphrasia* (p.s.); **Cistaceae:** *Helianthemum* (p.s.); **Lamiaceae:** *Acinos* (Ebmer 1984), *Thymus* (Ebmer 1984); **Linaceae:** *Linum* (p.s.).
Dufourea paradoxa (Morawitz, 1867)	**Crassulaceae:** *Sempervivum* (p.s.); **Orobanchaceae:** *Euphrasia* (Friese 1898, Ebmer 2003, p.s.); **Lamiaceae:** *Thymus* (p.s.); **Asteraceae:** *Hieracium* (Frey-Gessner 1899–1907, Ebmer 1984, Dylewska 1993), *Leontodon* (Bossert 2014); **Cistaceae:** *Helianthemum* (p.s.); **Caryophyllaceae:** *Silene* (Friese 1898); **Rosaceae:** *Potentilla* (Dylewska 1993, p.s.); **Primulaceae:** *Soldanella* (p.s.); **Saxifragaceae:** *Saxifraga* (p.s.); **Salicaceae:** *Salix* (p.s.); **Campanulaceae:** *Phyteuma* (Ebmer 1984); **Plantaginaceae:** *Veronica* (Friese 1898).
Megachile (*Megachile*) *alpicola* Alfken, 1924	**Fabaceae:** *Lathyrus* (Dorn and Weber 1988, p.s.), *Lotus* (Stoeckhert 1933, Dorn and Weber 1988, Westrich 1989, p.s.), *Medicago* (Dorn and Weber 1988, p.s.), *Trifolium* (p.s.), *Vicia* (Dorn and Weber 1988, p.s.); **Asteraceae:** *Centaurea* (Dylewska 1993), *Cirsium* (Westrich 1989), *Hieracium* (Westrich 1989), *Leontodon* (Westrich 1989, Dylewska 1993); **Cistaceae:** *Helianthemum* (p.s.); **Asparagaceae:** *Anthericum* (p.s.); **Ranunculaceae:** *Ranunculus* (Dorn and Weber 1988); **Clusiaceae:** *Hypericum* (p.s.); **Orobanchaceae:** *Odontites* (p.s.); **Plantaginaceae:** *Plantago* (Westrich 1989), *Veronica* (p.s.); **Alliaceae:** *Allium* (p.s.); **Rosacae:** *Potentilla* (p.s.); **Dipsacaceae:** *Scabiosa*) (p.s.); **Lamiaceae:** *Thymus* (Stoeckhert 1933, Dorn and Weber 1988, Westrich 1989); **Salicaceae:** *Salix* (p.s.).
Megachile (*Xanthosarus*) *analis* Nylander, 1852	**Campanulaceae:** *Campanula* (Alfken 1913, Stoeckhert 1933, Dorn and Weber 1988, Westrich 1989, p.s.), *Phyteuma* (p.s.); **Fabaceae:** *Hippocrepis* (p.s.), *Lotus* (Alfken 1913, Stoeckhert 1933, Dorn and Weber 1988, Westrich 1989, p.s.), *Onobrychis* (Westrich 1989, p.s.), *Trifolium* (Dorn and Weber 1988, Westrich 1989), *Vicia* (Dorn and Weber 1988); **Cistaceae:** *Helianthemum* (p.s.); **Orobanchaceae:** *Odontites* (p.s.); **Resedaceae:** *Reseda* (p.s.); **Ericaceae:** *Erica* (Alfken 1913, Benno 1952, Dorn and Weber 1988, Westrich 1989).
Hoplitis (*Anthocopa*) *villosa* (Schenck, 1853)	**Asteraceae:** *Centaurea* (Stoeckhert 1954, Franz 1982, Westrich 1989, p.s.), *Cichorium* (Westrich 1989), *Cirsium* (Westrich 1989), *Crepis* (Westrich 1989), *Hieracium* (Westrich 1989), *Leontodon* (Westrich 1989, Dylewska 1993, Bossert 2014), *Picris* (Westrich 1989), *Tanacetum* (Westrich 1989), *Tragopogon* (Zettel et al. 2005); **Geraniaceae:** *Geranium* (p.s); **Cistaceae:** *Helianthemum* (p.s.).
Osmia (*Helicosmia*) *labialis* Pérez, 1879	**Asteraceae:** *Carduus* (Tkalců 1975, Ebmer 2001, Herrmann 2010), *Centaurea* (Ebmer 2001, Herrmann 2010, Kraus 2010, p.s.), *Hieracium* (Ebmer 2001); **Cistaceae:** *Helianthemum* (p.s.).
Osmia (*Melanosmia*) *alticola* Benoist, 1922	**Fabaceae:** *Anthyllis* (p.s.), *Hippocrepis* (p.s.), *Lotus* (p.s.), *Trifolium* (p.s.).

Bee species	Pollen host genera
Osmia (*Melanosmia*) *inermis* (Zetterstedt, 1838)	**Fabaceae:** *Anthyllis* (p.s.), *Astragalus* (Elfving 1968), *Hippocrepis* (Stoeckhert 1933, Westrich 1989, p.s.), *Lotus* (Frey-Gessner 1908–1912, Schedl 1982, Westrich 1989, p.s.), *Onobrychis* (Westrich 1989); **Ericaceae:** *Vaccinium* (Elfving 1968, Hicks 2009, Stoeckhert 1933, Westrich 1989, p.s.); **Rosaceae:** *Geum* (Elfving 1968, Schedl 1982), *Potentilla* (Frey-Gessner 1908–1912, p.s.); **Salicaceae:** *Salix* (Stubbs in Hicks 2009).
Osmia (*Melanosmia*) *parietina* Curtis, 1828	**Fabaceae:** *Anthyllis* (p.s.), *Hippocrepis* (Stoeckhert 1933, Westrich 1989, p.s.), *Lotus* (Westrich 1989, p.s.), *Trifolium* (Blüthgen 1952, p.s.); **Lamiaceae:** *Ajuga* (Stoeckhert 1933); **Cistaceae:** *Helianthemum* (p.s.); **Rosaceae:** *Fragaria* (Blüthgen 1952), *Potentilla* (p.s.); **Crassulaceae:** *Sedum* (Westrich 1989).
Osmia (*Melanosmia*) *steinmanni* Müller, 2002	**Fabaceae:** *Hippocrepis* (p.s.), *Lotus* (p.s.), *Trifolium* (p.s.); **Ericaceae:** *Rhododendron* (p.s.).
Osmia (*Melanosmia*) *uncinata* Gerstaecker, 1869	**Fabaceae:** *Anthyllis* (p.s.), *Hippocrepis* (Westrich 1989, p.s.), *Lotus* (Stoeckhert 1933, Westrich 1989, Dylewska 1993, p.s.), *Lathyrus* (Stoeckhert 1933, Westrich 1989, p.s.), *Medicago* (p.s.), *Onobrychis* (Westrich 1989, p.s.), *Trifolium* (Westrich 1989, p.s.), *Vicia* (Westrich 1989, p.s.); **Rosaceae:** *Fragaria* (Stoeckhert 1933, *Potentilla* (Stoeckhert 1933, Westrich 1989, p.s.), *Rosa* (Stoeckhert 1933), *Rubus* (Westrich 1989); **Lamiaceae:** *Ajuga* (Stoeckhert 1933), *Glechoma* (Westrich 1989), *Salvia* (Westrich 1989); **Plantaginaceae:** *Plantago* (p.s.), *Veronica* (p.s.); **Alliaceae:** *Allium* (p.s.); **Ranunculaceae:** *Ranunculus* (Westrich 1989); **Caprifoliaceae:** *Lonicera* (p.s.); **Boraginaceae:** *Echium* (p.s.), *Pulmonaria* (Westrich 1989); **Cistaceae:** *Helianthemum* (Westrich 1989, p.s.); **Asteraceae:** *Hieracium* (Stoeckhert 1933), *Leontodon* (Dylewska 1993), *Taraxacum* (Stoeckhert 1933, Westrich 1989); **Cornaceae:** *Cornus* (Westrich 1989); **Ericaceae:** *Vaccinium* (Stoeckhert 1933, Westrich 1989); **Salicaceae:** *Salix* (Stoeckhert 1933, Westrich 1989).
Osmia (*Melanosmia*) *xanthomelana* (Kirby, 1802)	**Fabaceae:** *Hippocrepis* (Stoeckhert 1933, Westrich 1989, p.s.), *Lotus* (Stoeckhert 1933, Westrich 1989, p.s.).

that among these three families flowers of *Sempervivum*, *Euphrasia* and *Thymus*, respectively, are the most important pollen hosts. In strong contrast to *Dufourea alpina*, flowers of Campanulaceae are only exceptionally exploited. Friese (1898) observed females visiting the flowers of *Veronica* (Plantaginaceae), suggesting that this genus is probably an additional pollen source.

Megachile (*Megachile*) *alpicola* Alfken, 1924

Megachile alpicola collected the pollen of 16 plant families (Tab. 1). Almost 75% of the pollen recorded in the female scopae originated from the flowers of Fabaceae and Asteraceae (Fig. 10). Among the Fabaceae, *Lotus* was by far the most important host, but pollen was also collected on several other genera. Among the Asteraceae, species of all three subfamilies were exploited for pollen. The four plant families listed by Westrich (1989) as pollen hosts were all confirmed in the present study.

Megachile (*Xanthosarus*) *analis* Nylander, 1852

Megachile analis had a distinctly narrower pollen diet than *M. alpicola* and restricted pollen collection mainly to species of Campanulaceae and Fabaceae (Tab. 1). Pollen of these two plant families contributed 95.3% to the total pollen grain volume. Field observations revealed that among the Campanulaceae both *Campanula* and *Phyteuma* are exploited for pollen. Among the Fabaceae, *Lotus* was by far the most important host, but pollen was also collected on other genera, such as *Hippocrepis* or *Onobrychis*. The strong preference of *M. analis* for Campanulaceae and Fabaceae as found in the present study conforms to field observations and pollen analytical studies by other authors (Alfken 1913, Benno 1952, Westrich 1989). In northern Europe, *M. analis* often visits the flowers of *Erica tetralix* L. (Ericaceae), which are forcefully exploited for nectar and possibly also serve as pollen source (Alfken 1913, Benno 1952, Haeseler 1980). In the pollen loads from the Alps, however, no pollen of Ericaceae was recorded.

Hoplitis (*Anthocopa*) *villosa* (Schenck, 1853)

Hoplitis villosa almost exclusively collected pollen on Asteraceae. In seven pollen loads, however, pollen of *Helianthemum* (Cistaceae) or *Geranium* (Geraniaceae) was recorded in addition to that of Asteraceae (Tab. 1), suggesting that pollen is rarely harvested also on plant taxa other than Asteraceae. Among Asteraceae, species of the subfamily Cichorioideae were by far the most important pollen hosts (Fig. 11), followed by representatives of the subfamily Carduoideae, whereas pollen of the subfamily Asteroideae was only exceptionally collected. These results are in line with pollen analytical studies by Westrich (1989), who categorized *H. villosa* as an Asteraceae oligolege that preferentially exploits species of the Cichorioideae.

Osmia (*Helicosmia*) *labialis* Pérez, 1879

Osmia labialis exclusively collected pollen on Asteraceae except for one specimen, whose pollen load additionally contained marginal amounts of pollen of *Helianthemum* (Cistaceae) (Tab. 1). Among the Asteraceae, it showed a near exclusive preference for pollen of the Carduoideae (Fig. 12) and only very rarely collected pollen on Cichorioideae and Asteroideae. All published flower records of *O. labialis* refer to species of the Carduoideae (Tkalců 1975, Ebmer 2001, Herrmann 2010, Kraus 2010), supporting the high importance of this subfamily in the species' larval diet. *O. labialis* appears to have a narrower pollen diet than its closest relative *Osmia leaiana* (Kirby), which also restricts pollen collection to the Asteraceae, but often also exploits Cichorioideae in addition to Carduoideae (Raw 1974, Westrich 1989, A. Müller unpublished data).

Osmia (*Melanosmia*) *alticola* Benoist, 1922

Osmia alticola exclusively harvested pollen on Fabaceae (Tab. 1). In contrast to the closely related *O. xanthomelana*, which only collected the pollen of *Hippocrepis*

and *Lotus* (see below), the diet of *O. alticola* was broader and encompassed the pollen of additional Fabaceae genera, such as *Anthyllis*, *Trifolium* and others. Due to the low number of pollen samples available, the categorization of *O. alticola* as a Fabaceae oligolege (Tab. 1) may appear premature. However, the fact that eight out of the 16 pollen loads analyzed consisted of mixtures of pollen of several Fabaceae genera clearly points to a strict pollen specialization at the family level.

Osmia (*Melanosmia*) *inermis* (Zetterstedt, 1838)

Osmia inermis collected the pollen of four plant families, but exhibited a strong preference for Loteae, particularly for *Lotus* and *Hippocrepis* (Tab. 1). These results are in line with Westrich (1989), who categorized *O. inermis* as being narrowly polylectic with a preference for Fabaceae, but do not support Stoeckhert (1933), who assumed *Vaccinium* to be the preferred pollen host. In Atlantic Canada and the northeastern United States, however, the species appears to be dependent primarily on Ericaceae (Hicks 2009). There, it occasionally also collects pollen on *Salix* (Salicaceae) (Stubbs in Hicks 2009).

Osmia (*Melanosmia*) *parietina* Curtis, 1828

Osmia parietina harvested the pollen of five plant families (Tab. 1). However, it exhibited a strong preference for Loteae, particularly for *Lotus* and *Hippocrepis* (Tab. 1, Fig. 13). Among the Fabaceae, *Trifolium* was also regularly exploited; its pollen was recorded in eleven pollen loads and contributed 7.4% to the total pollen grain volume. *Sedum* (Crassulaceae) is listed as an additional pollen source by Westrich (1989), and *Veronica* (Plantaginaceae) might possibly be a further pollen host based on the observations by Blüthgen (1952).

Osmia (*Melanosmia*) *steinmanni* Müller, 2002

Osmia steinmanni had a strong affinity for Fabaceae (Tab. 1) and collected pollen mainly on *Hippocrepis* and *Lotus*, more rarely on *Trifolium*. One load additionally contained substantial amounts of pollen of *Rhododendron* (Ericaceae). In spite of the low number of pollen loads available, these findings suggest that *O. steinmanni* has very similar pollen host preferences as its close relative *O. inermis* (see above). More pollen loads are needed both to clarify the significance of Ericaceae in the pollen diet of *O. steinmanni* and to examine whether pollen of plant families other than Fabaceae and Ericaceae is occasionally also harvested.

Osmia (*Melanosmia*) *uncinata* Gerstaecker, 1869

Osmia uncinata harvested the pollen of eleven plant families (Tab. 1), but exhibited a strong preference for Fabaceae, which - however - was less pronounced than in the other *Osmia* species of the subgenus *Melanosmia* investigated in the present study. Among the Fabaceae, *Lotus*, *Hippocrepis* and *Trifolium* were the predominant pollen sources, but other Fabaceae genera were also exploited. Moderately important pollen hosts were species of Rosaceae and Lamiaceae, whose pollen contributed about 10% and 7%, respectively, to the total pollen grain volume (Fig. 14). Thus, *O. uncinata* is the least specialized species of the subgenus *Melanosmia* both in terms of the number of plant families and the number of Fabaceae genera exploited. Westrich (1989) lists pollen hosts belonging to ten plant families, among which Asteraceae, Cornaceae, Ericaceae and Salicaceae were not recorded in the pollen loads analysed in the present study. Based on the observations by Stoeckhert (1933), pollen might occasionally also be collected on *Polygala* (Polygalaceae) and *Viola* (Violaceae).

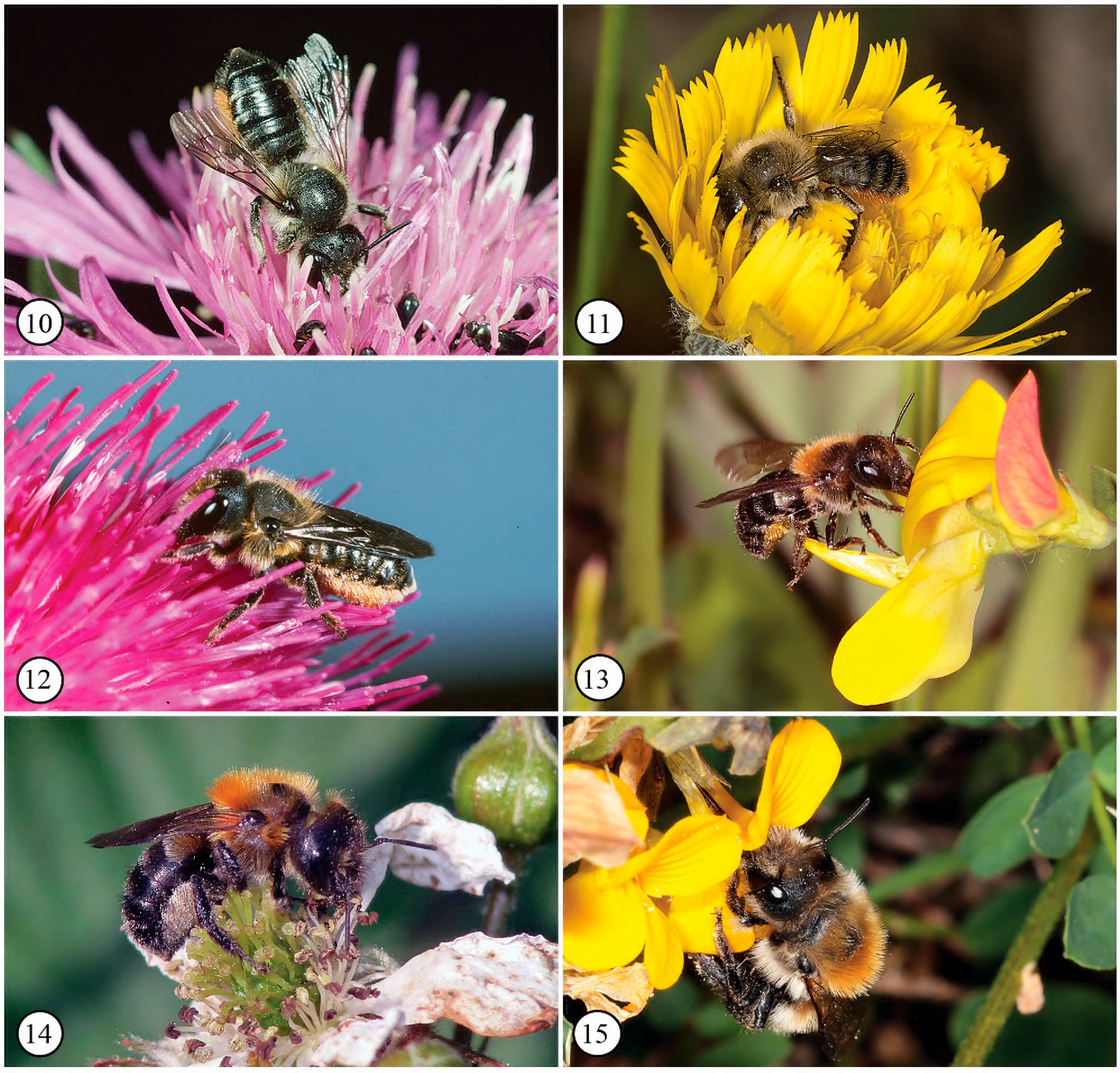
Osmia (*Melanosmia*) *xanthomelana* (Kirby, 1802)

Osmia xanthomelana exclusively collected pollen on *Hippocrepis* and *Lotus* (Fabaceae) (Tab. 1, Fig. 15), rendering this species the most specialized among the *Osmia* (*Melanosmia*) species examined in the present study. The strict dependence of *O. xanthomelana* on only two Fabaceae genera of the tribe Loteae was already supposed by Westrich (1989). In contrast, the assumption of Stoeckhert (1933) that *O. xanthomelana* also harvests pollen on other taxa than *Hippocrepis* and *Lotus* is not supported by the results of the present study.

Discussion

The 19 bee species investigated in the present study widely vary in their pollen host spectra and degree of host plant specialization, revealing a fascinating diversity in bee pollen host use (Tab. 1). The examined set of species encompasses i) narrowly oligolectic species, which exclusively collect pollen on a single plant genus, ii) broadly oligolectic species, which harvest pollen on a single plant family, iii) mesolectic species, which are dependent on two plant families, iv) polylectic species, which exhibit a strong but not exclusive preference for a single plant taxon, and v) polylectic species, which do not prefer any single plant taxon and exploit up to 17 different plant families.

Comparison of pollen host use among closely related species of the same subgenus or the same monotypic genus reveals different patterns (see species accounts above and Tab. 1). The six *Osmia* species of the subgenus *Melanosmia* all exhibit a pronounced affinity for the pollen of Fabaceae, supporting other studies which demonstrated that host plant preferences are often conserved in clades of closely related bee species (Müller 1996, Wcislo and Cane 1996, Michez et al. 2004, Sipes and Tepedino 2005, Patiny et al. 2007, Larkin et al. 2008, Michez et al. 2008, Sedivy et al. 2008, 2013). However, the degree of dependence on Fabaceae pollen differs among the *O.* (*Melanosmia*) species, ranging from a narrow specialization on Fabaceae as in *O. xanthomelana*, which collects pollen solely from the flowers of two closely related Fabaceae genera, to a moderately strong dependence on Fabaceae as in *O. uncinata*, which exploits the flowers of at least 14 additional plant families. In contrast to *O.* (*Melanosmia*), the three *Andrena* species of the subgenus *Andrena* wide-



Figures 10–15. (**10**) *Megachile alpicola* on *Centaurea jacea* L. (photo A. Krebs). (**11**) *Hoplitis villosa* on *Taraxacum* spec. (photo P. Westrich). (**12**) *Osmia labialis* on *Carduus nutans* L. (photo A. Krebs). (**13**) *Osmia parietina* on *Lotus corniculatus* L. (photo R. Prosi). (**14**) *Osmia uncinata* on *Rubus* spec. (photo A. Jacobs). (**15**) *Osmia xanthomelana* on *Hippocrepis comosa* L. (photo R. Prosi).

ly differ in their pollen host use as do the two *Dufourea* species. While the differences between *A. fucata* and *A. rogenhoferi* are potentially due to deviating distribution and habitat selection with *A. fucata* restricted to forested areas of the montane and subalpine zone and *A. rogenhoferi* colonizing a wide spectrum of habitats from the submontane to the alpine zone (SwissBeeTeam 2018), the pronounced preference of *A. lapponica* for Ericaceae pollen might possibly be genetically based as it is the case for other bee species with a specialized diet (Praz et al. 2008). A genetic basis for the differing pollen host choice is also suggested for the two *Dufourea* species, which often colonize the same habitats in the Alps, where they encounter a similar flower supply but nevertheless collect the pollen of different plant taxa. For both *Panurginus* species, pollen of *Potentilla* (Rosaceae) plays an important role in the larval diet. Interestingly, *P. herzi* is entirely dependent on *Potentilla*, whereas *P. montanus* is capable of exploiting several additional hosts. If future studies show that the polylectic habit of *P. montanus* is evolutionary derived, this would support the view that many generalist bee species that evolved from specialized ancestors had broadened their diet under maintenance of the exclusive host of their ancestors (Sedivy et al. 2008).

Acknowledgements

I gratefully acknowledge the help of the following colleagues who generously permitted pollen removal from bee specimens of their collections or under their curation: F. Amiet (Solothurn), G. Artmann (Olten), H. Baur

(Naturhistorisches Museum Bern), M. Bur (Rechthalten), R. Eastwood (ETH Zürich), K. Hirt (Menziken), A. Freitag (Musée de Zoologie Lausanne), F. Gusenleitner and M. Schwarz (Biologiezentrum Linz), M. Herrmann (Konstanz), S. Liersch (Bündner Naturmuseum Chur), R. Neumeyer (Zurich), C. Praz (Université de Neuchâtel) and C. Schmid-Egger (Berlin). Katharina Bieri (Biological Institute for Pollen Analysis, Kehrsatz) kindly helped with the identification of several difficult pollen types. D. Bénon, S. Falk, A. Jacobs, A. Krebs, W. Kreisch, H.-J. Martin, R. Prosi and P. Westrich provided photos. Comments by J. Litman, M. Kuhlmann, C. Praz and V. Mauss improved the manuscript. The project was generously funded by the Tierschutzverein Glarus.

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